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Biometric and chemical analysis of five herbs in a regional acid-base gradient in Swedish beech forest soils

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ABSTRACT

Mercurialis perennis, Galium odoratum, Stellaria nemorum, Oxalis acetosella and *Maianthemum bifolium* were studied in beech forest soils of different chemistry. Six to ten stands were chosen for each species, representing their pH-range in southern Sweden. Plots of 0.25 m^2 were intensively studied for species performance (number of shoots, leaves; height; cover; flowering; leaf concentration of thirteen elements) and related to the chemistry of the surface soil (pH; base saturation; exchangeable K, Na, Ca, Mg, Mn, Zn; clay and organic matter content).

Information was obtained on the intra- and inter-species variation. The leaf concentrations differed significantly among the species for most elements and the intra-species variation was explained by different soil characteristics. Soil chemistry explained much of the variability in the species performance (cover, above-ground biomass), while the leaf concentrations seemed to be most important to *M. perennis*.

KEYWORDS: beech forest, pH-gradient, plant performance, growth, flowering, soil chemistry, leaf chemistry.

RÉSUMÉ

Mercurialis perennis, Galium odoratum, Stellaria nemorum, Oxalis acetosella et *Maianthemum bifolium*, provenant de sols de hêtraies aux propriétés chimiques différentes ont été étudiées. Pour chaque espèce, six à dix stations ont été choisies, représentant un échantillonnage de leur pH au sud de la Suède. Des parcelles de 0,25 m^2 ont été intensivement étudiées quant aux performances de chaque espèce (nombre de racines, de feuilles; hauteur; recouvrement; floraison; concentration foliaire de 13 éléments) et en liaison avec la chimie du sol de surface (pH; saturation en bases; K, Na, Ca, Mg, Mn, Zn échangeables; teneur en argile et matière organique).

Des données sur les variations intra- et interspécifiques ont été obtenues. D'une espèce à l'autre, les concentrations en éléments dans les feuilles varient significativement et il existe des différences intraspécifiques liées aux variations des caractéristiques du sol. La chimie du sol explique en grande partie la variabilité des performances des espèces (couvert, biomasse épigée), les concentrations en éléments dans les feuilles semblant être les plus importantes chez *M. perennis*.

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INTRODUCTION

It has long been known that the distribution of many plant species is highly correlated with soil pH (e. g. OLSEN, 1921). Acidophilic species show a higher cover at lower pH values while more demanding species often increase in cover with increasing pH. Acidification of soils has appeared to accelerate during the last few decades in south Sweden (HALLBÄCKEN & TAMM, 1986; FALKENGREN-GRERUP, 1986, 1987; TAMM & HALLBÄCKEN, 1988; FALKENGREN-GRERUP & ERIKSSON, 1990). Many species seem to have become more tolerant to acid soils, as judged by increases in frequency and cover values that occurred (FALKENGREN-GRERUP, 1986; 1989 *a*; 1990), which may partly be explained by increased nitrogen deposition, that was earlier a limiting nutrient in many forest ecosystems.

Macronutrients are leached out of acidified soils. Up to 50% of the exchangeable base cations (Ca, Mg, K, Na) and Zn were lost and exchangeable Al increased over 35 years in southern Swedish soils (FALKENGREN-GRERUP *et al.*, 1987; FALKENGREN-GRERUP, 1989 *b*). As many herbs and grasses increased in cover, these nutrients have probably not been limiting, at least not at intermediate or higher pH values of their range. Current studies indicate that only a few species have more than a limited occurrence on the most acid beech forest soils (pH (H_2O) ca. 4.0), especially on mor soils (FALKENGREN-GRERUP, 1990).

The object of this paper is to study how species are responding to an acid-base gradient of the surface soil. Five species were analyzed in a regional soil gradient in Skåne (the southernmost province of Sweden), namely *Galium odoratum*, *Maianthemum bifolium*, *Mercurialis perennis*, *Oxalis acetosella* and *Stellaria nemorum*. Cover and other indicators of performance (height, number of leaves and shoots, flowering, rhizomes) and nutrient concentrations of the leaves, were analyzed. The parameters were related to the chemical properties of the surface soil.

MATERIALS AND METHODS

The distribution of *O. acetosella* and *M. bifolium* encompasses all of Sweden, while *G. odoratum* and *M. perennis* are restricted to the south of the country (latitude < 60°, HULTÉN, 1971). *S. nemorum* has two subspecies, *glochidosperma*, being mainly found in Skåne (latitude < 56°), and *nemorum* (or *montana*), found throughout Sweden. Within a pH (KCl) interval of 2.8-4.5 in southern Swedish beech forests, *M. bifolium* has its peak cover at 3.2, *O. acetosella* at 3.6 and the three other species above 3.8 (FALKENGREN-GRERUP, 1989 *a*). Corresponding values for oak/hornbeam forests in southern Sweden are 0.2-0.6 pH units higher (TYLER, 1989).

Utilizing a current project of flora relationships and chemical soil properties in beech forests in Skåne (TYLER, 1987), stands along a pH gradient of soils were chosen for the five quantitatively important species *G. odoratum*, *M. bifolium*, *M. perennis*, *O. acetosella* and *S. nemorum* (fig. 1). This project was able to provide data on pH (composite sample from ten 5 m^2 plots; 10.0 g fresh soil to 50 ml 0.2 M KCl) and clay content. Species cover was visually estimated in ten plots (5 m^2) for each stand, using percentage classes (1-15%, 16-25%, 26-35%, etc.).

A pilot study was undertaken in 1986 and the main study in 1987. In 1986, four stands (six for *O. acetosella*) were used. In each stand, a small plot (0.5 × 0.5 m) was subjectively chosen for species under investigation, representing high cover, well developed shoots and a high degree of flowering. The selection of the "best" plot was made to give the possibility of a maximum response of the species. All stands had a tree cover of at least 70%. Cover was recorded in 5%-classes and the number of shoots of the studied species was counted. The plants were excavated with roots and rhizomes as intact as possible. After rinsing, the plants were laid out between paper sheets at a temperature of 40 C for later measurement of shoots (height, weight, number of leaves, flowering, number of shoots per rhizome) and rhizome weight.

O. acetosella was excluded from the main study in 1987 because of limited resources. Ten stands, each with two small plots chosen as above, were studied for the four remaining species. Some stands were chosen for more than one species (2 stands for 3 species, 8 stands for 2 species). The same measurements as in 1986 (except weight) were used for a minimum of 40 shoots per plot. In stands with a small cover of the species, fewer shoots had to be accepted (1 stand for *G. odoratum* and *M. perennis*, 3 stands for *S. nemorum*). The number of shoots for *O. acetosella* was always larger than 75.

In 1987, chemical analyses were made of soil and leaves. Four cores (each 192.5 cm^3 of 5 cm depth below litter layer) were taken around the small plot and combined to a composite sample. 10 g fresh soil of <2 mm fraction was shaken for 2 hours in 50 ml 0.2 M KCl and pH measured electrometrically in the supernatant after settlement over night. To measure exchangeable cations, 10 g fresh soil was extracted with 50 ml M ammonium acetate, pH 7.00. The filtrates were analyzed for Na, K, Mg, Ca, Mn, and Zn, by plasma emission spectroscopy (ICP).

Chemical analysis was made on non-flowering plants collected close to the small plot. In stands with a low cover of the studied species, one instead of two collections of plant material was utilized (1 stand for *M. bifolium*, 2 for *G. odoratum*, *S. nemorum*, 3 for *M. perennis*). The plants were dried to 40°C after collection and to constant weight in 85°C before analysis. The green leaves (0.5-1.0 g) were wet digested in 20 ml concentrated HNO_3 and analyzed by ICP. Nitrogen was analyzed by the Kjeldahl method (including *O. acetosella*).

Abbreviations used in the text are defined in table I.

TABLE I. — *Definitions of the abbreviations used.*

Small plot	0.25 m^2
Large plot	500 m^2
Cover	Visual estimate of covered horizontal area (%)
No. of shoots m^{-2}	Number of shoots m^{-2} counted in the small plot
No. of shoots m^{-2} in covered area	Ratio of (No. of shoots m^{-2}): (Small plot cover)
Shoot height	Height (mm) of green shoot and inflorescence. *O. acetosella:* heights of all leaf and flower stalks emanating from one petiole base.
Shoot × height	No. of shoots m^{-2} × average shoot height
No. of leaves	Number of single leaves (*M. bifolium*, *O. acetosella*), pairs (*S. nemorum*, *M. perennis*) or whorls (*G. odoratum*).
No. of shoots rhizome^{-1}	Number of shoots connected to one rhizome
Above-ground weight	Average weight (mg) of >40 shoots from the small plot. *O. acetosella:* weights of all leaf and flower stalks emanating from one petiole base.
Below-ground weight	Average weight (mg) for rhizomes and roots. One rhizome may carry more than one shoot.
Above: below-ground ratio	Ratio of above-ground and below-ground weights.
Flowering	Percentage of flowering shoots. *O. acetosella:* percentage of petiole bases with flowers.

RESULTS

In the current study of 95 beech forests in Skåne, *M. perennis* and *G. odoratum* were found on soils with relatively high pH and low organic matter content (fig. 1). *S. nemorum* was restricted to mull soils but, unlike the previous species, had highest cover in the middle of its pH range. *O. acetosella* had a wide pH tolerance and occurred in 80% of the stands. Except for the extreme ends of the range, the cover was relatively high along the whole gradient. *M. bifolium* grew in the most acid and humus rich part of the gradient with maximum cover at lower pH values than for *O. acetosella*.

Comparing soil pH of the two small plots with the surrounding large plot, the small plots of *M. perennis* and *G. odoratum* had significantly higher values (table II). *S. nemorum* was found on somewhat higher pH and *M. bifolium* on slightly lower pH than measured for the large plot.

As the small plots were selected for the best possible growth of the species, the cover was several times higher than for the large plot (table III). This was especially evident for *M. perennis*, a species that can grow very densely even in stands with a low average cover. The flowering frequency varied a lot between the species, being highest for *S. nemorum* and lowest for *O. acetosella* and *M. bifolium*. Several of the other parameters in table III describe the morphological characters of the species, fluctuating around the mean depending on the environment.

The linear correlation between shoot height and weight was highly significant for all species in the pilot study: *M. bifolium*, *M. perennis* ($r=0.67$-0.70), *G. odoratum*, *S. nemorum*, *O. acetosella* (0.87-0.89, $n=119$-489). The above: below-ground ratio depends on the number of shoots per rhizome as well as on the morphology. *S. nemorum* had the highest ratio in spite of only 1.4 shoots being connected to a rhizome, but the rhizomes are thin, as for *G. odoratum*, and the shoots can grow densely to a considerable height.

The leaf concentrations of the 13 analyzed elements differed substantially among the species (table IV). The highest concentrations were measured in *M. perennis* and *S. nemorum* and the lowest in *M. bifolium*. All elements but Mg, Mn and B were found in lowest concentrations in this species. *S. nemorum* had especially high levels of Na and Mn. The soil properties for *M. perennis*, *G. odoratum* and *S. nemorum* were not significantly different.

To what extent are the soil properties reflected in the leaf concentrations of the same or related elements? Ca, Mg and Na in leaves were often significantly correlated to soil variables, however not always to the corresponding element in the soil (table V). This means that the soil-leaf relationships were not consistent for all species. The leaf concentration of Mn was always negatively related to soil pH or base saturation. Organic matter content was related to leaf concentrations of several elements for all species. The clay content seemed to be most important for *G. odoratum*, being negatively related to four of the leaf elements.

The relationships between growth, soil and leaf chemistry are shown in table VI. The highest multiple correlation coefficients were found for cover, number of shoots m^{-2}, shoot × height and shoot height. Flowering frequency had among the lowest coefficients, but still significant. The soil and leaf variables were of different importance for the biometric measurements. The flowering was exclusively related to the soil variables, and shoot × height and number of shoots $rhizome^{-1}$

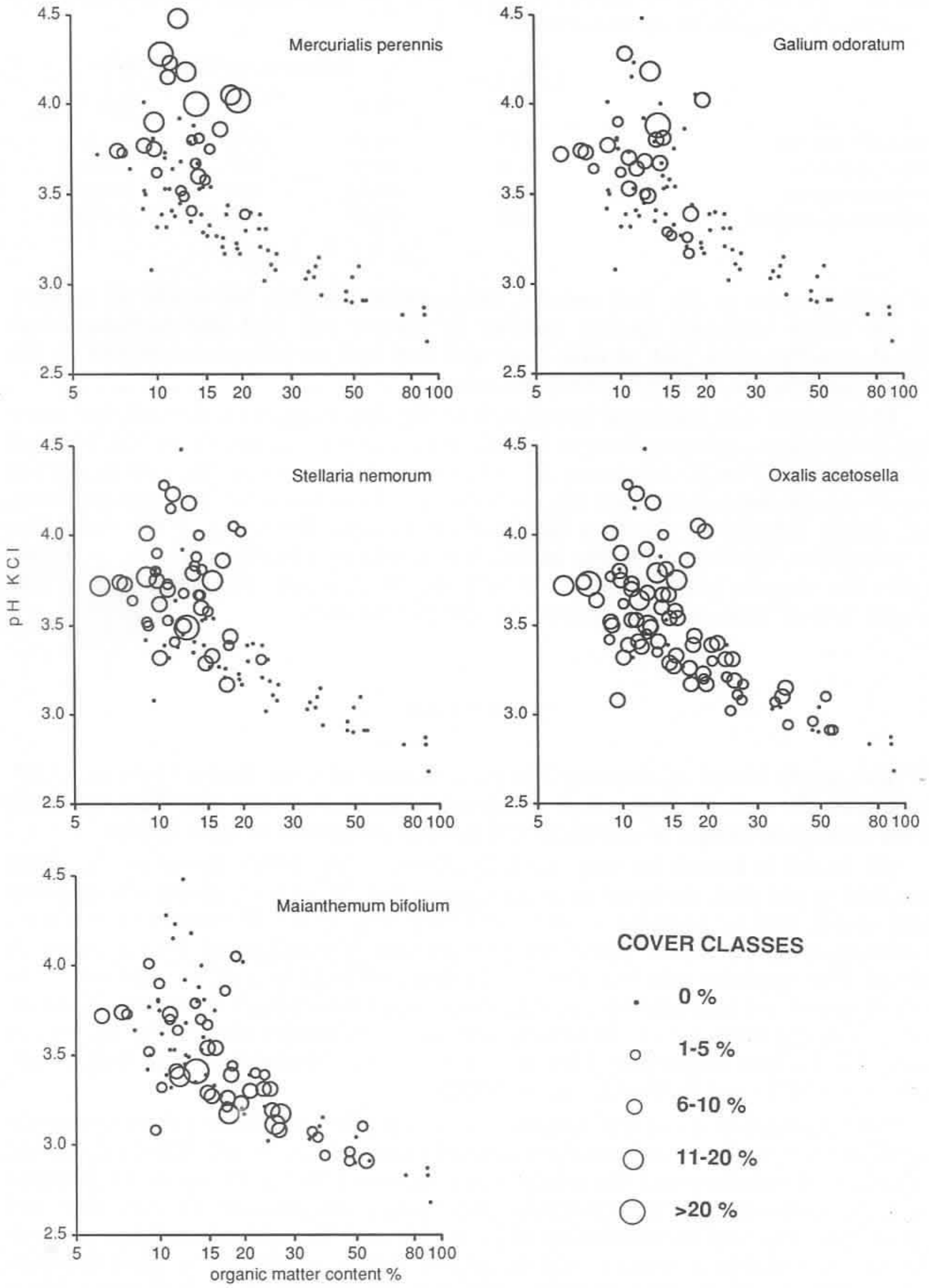

FIG. 1. – Cover (%) of five species in 95 beech forests in southern Sweden, related to organic matter content and pH (0.2 M KCl) in the topsoil (0-5 cm).

TABLE II. – *pH (KCl) of the top soil* (0-5 *cm*) *of the large plots and difference between small* ($n=20$) *and large* ($n=10$) *plots for the studied species.*

	Large plot	Difference small-large plot		
	Mean	Mean	Stdev	Sign. level
Mercurialis perennis	3.77	+0.28	0.45	$p<0.011$
Galium odoratum	3.70	+0.26	0.27	$p<0.001$
Stellaria nemorum	3.67	+0.12	0.26	$p<0.063$
Maianthemum bifolium	3.48	−0.08	0.17	$p<0.053$

had soil variables as the first entered independent variable for nearly all species. For the other variables (except number of leaves) soil and leaf nutrients were entered equally often, but usually both soil and leaf variables contributed to the multiple correlation coefficient to some extent.

M. perennis was positively correlated to the clay content of the soil, but more often to nutrient concentrations in leaves, among others negatively to Na, Mn and positively to Sr. For *G. odoratum*, *M. bifolium* and *S. nemorum* the soil properties were of greater importance than the leaf concentrations in explaining plant performance, being entered as the first independent variable for most of the biometric measurements. Exchangeable Na in soil was positively correlated for *G. odoratum* as was the organic matter content in soil for *M. bifolium*. No single leaf or soil variable was of more general importance for *S. nemorum*.

DISCUSSION

This study aimed at showing the performance of some forest herbs in a pH-gradient in the soil. By doing this, substantial information has also been obtained on the ecological ranges of chemical and growth properties of each species.

pH in soil is known to vary spatially (BRINGMARK, 1989). However, the small plots had a pH that deviated in a systematic way from that of the surrounding beech stand. Species growing in soils with relatively high pH values (*M. perennis*, *G. odoratum*) had a higher pH in the surface soil than measured for the stand in general. The opposite was true for *M. bifolium*, growing in a more acid soil. This study does not explain whether the difference in pH determined the species distribution or was the outcome of the species presence, but species can acidify the soil as shown for *Calluna vulgaris* by GRUBB and SUTER (1971) and for some forest trees NIHLGÅRD (1971) and BERGKVIST *et al.* (1987).

The concentrations of leaf nutrients were specific and differed from species to species in spite of the co-existence on several plots and the small differences in soil properties. *M. bifolium* had the lowest leaf concentration for 10 out of 13 elements and some elements differed markedly also among *M. perennis*, *G. odoratum* and *S. nemorum*. The leaf concentration of N, K, Ca and Mg seldom varied more than a factor two within a species, which, except for N, is similar to East German studies (HÖHNE, 1962). Phosphorous, Mn and Na varied up to 5-10 times. Even larger differences were found among the species. Large intra-species variation was also found for Al, as shown in other studies (TYLER, 1976; FOLKESON *et al.*, 1990).

TABLE III. — *Averages of biometric parameters of the small ($n=17-20$) and large ($n=10$) plots (4 small plots for weights). Standard deviation is given in small figures. The ratio of small/large plot cover is calculated from the mean ratios of each plot (geometric mean).*

	Mercurialis perennis	*Galium odoratum*	*Stellaria nemorum*	*Oxalis* (¹) *acetosella*	*Maianthemum bifolium*
Small plot cover (%)	70^{23}	32^{17}	45^{15}	58^{23}	31^{24}
Large plot cover (%)	13^{13}	10^{9}	9^{4}	7^{3}	6^{3}
Small/large plot cover	11^{3}	5^{3}	5^{2}	8^{2}	5^{3}
No. of shoots m^{-2}	130^{56}	205^{168}	202^{103}	1269^{604}	251^{266}
No. of shoots m^{-2} of covered area	183^{50}	619^{217}	437^{165}	2104^{318}	690^{227}
No. of shoots rhizome^{-1}	$2.5^{0.8}$	$2.8^{1.0}$	$1.4^{0.3}$	$2.9^{0.9}$	$1.5^{0.3}$
Shoot height (mm)	200^{61}	163^{36}	218^{54}	112^{23}	67^{17}
No. of leaves (²)	$4.0^{0.4}$	$3.6^{0.3}$	$6.8^{0.8}$	–	$1.0^{0.1}$
Flowering frequency	27^{15}	13^{18}	45^{20}	7^{6}	7^{8}
Above-ground weight (mg)	295^{76}	79^{39}	189^{78}	17^{4}	71^{10}
Below-ground weight (mg)	2231^{1778}	200^{150}	50^{22}	106^{33}	185^{59}
Above/below-ground ratio	$0.6^{0.1}$	$1.6^{0.3}$	$5.0^{1.4}$	$0.5^{0.2}$	$0.7^{0.1}$

(¹) $n=6$ for small and large plots.

(²) *O. acetosella* and *M. bifolium* have one leaf per petiole; *M. bifolium* has two when flowering.

TABLE IV. – *Average leaf concentration (mg g^{-1}) of the studied species and the soil* (0-5 *cm*) *properties around the small plots* (*n*=17–20). *Standard deviation is given in small figures. Soil extraction was made in M NH$_4$Ac, pH* 7.00. *Clay content was measured for the large plots* (*n*=10). *The species with the highest average value of a leaf element is given in* **bold figures.**

	Mercurialis perennis		*Galium odoratum*		*Stellaria nemorum*		*Maianthemum bifolium*	
LEAF								
K	38.4	3.2	37.1	6.2	**52.0** (*)	8.5	32.5 (*)	6.8
N	38.6	4.9	37.0	5.9	**40.5**	4.8	25.0 (*)	2.7
Ca	**19.2** (*)	6.9	15.4 (*)	2.8	11.9 (*)	1.7	5.6 (*)	1.3
P	2.22	0.60	2.79	1.19	**4.37** (*)	1.34	1.84 (*)	0.24
Mg	**4.88** (*)	1.08	3.57 (*)	0.66	4.19	0.89	4.10	0.75
S	**5.33** (*)	1.48	3.35 (*)	0.66	2.78 (*)	0.35	1.86 (*)	0.29
Mn	0.309	0.27	0.415	0.26	**2.27** (*)	1.48	1.48 (*)	0.57
Fe	0.119 (*)	0.018	**0.221** (*)	0.148	0.142 (*)	0.039	0.100 (*)	0.020
Zn	**0.144** (*)	0.031	0.051 (*)	0.017	0.097 (*)	0.031	0.024 (*)	0.006
Al	0.093	0.038	**0.209** (*)	0.139	0.099	0.033	0.064 (*)	0.017
Na	0.108 (*)	0.039	0.080 (*)	0.035	**0.803** (*)	0.199	0.042 (*)	0.022
B	**0.047** (*)	0.009	0.032	0.015	0.030	0.011	0.037	0.007
Sr	**0.048**	0.026	0.035	0.021	0.023 (*)	0.006	0.015 (*)	0.004
SOIL								
CEC (uekv/g dw)	176	42	163	37	153	19	200	140
Organic matter content (% d.w)	14.9	4.6	13.5	4.2	13.4	2.4	20.8	15.7
pH (KCl)	4.04	0.54	3.94	0.49	3.80	0.41	3.41 (*)	0.27
base saturation (%)	40.7	15.2	40.2	14.2	31.8	12.5	18.7	6.0
Ca % CEC	30.7	13.7	30.1	12.8	23.7	10.7	12.0 (*)	4.7
Mg % CEC	5.81	2.36	5.24	2.21	4.41	2.03	3.11 (*)	0.95
K % CEC	3.01	0.85	3.52	0.74	2.44	0.84	2.36	0.58
Mn % CEC	0.88	0.93	1.01	0.80	0.92	0.65	0.92	0.36
Na % CEC	0.34	0.13	0.42	0.22	0.27	0.09	0.34	0.12
Zn % CEC	0.0285	0.0077	0.0286	0.0092	0.0245	0.0084	0.0211	0.0052
Clay content (%)	9.1	8.0	12.1	8.9	7.4	8.6	4.4	2.1

(*) Significant ($p<0.05$) difference from all other species (Student's *t*-test)

The relationships between soil and leaf concentrations are quite consistent, such as for Ca, Mn and often Mg (MENGEL & KIRKBY, 1982). In this study the leaf concentration of Mn was inversely related to pH or the base saturation of the soil for all species. This is found for various plants in both laboratory studies and natural ecosystems (OLSEN, 1934; TYLER, 1976; FOLKESON *et al.*, 1990). Manganese may be toxic at high concentrations, even if this is seldom the case for species growing on acid soils, being tolerant or even demanding of high concentrations (RORISON, 1986).

Physiological experiments can isolate and expand problems found in nature. Many species grow best at the highest pH used, values that may well exceed those in their natural habitats. *M. perennis* grew for example better at pH 7.5 – a value well above findings in this paper – than at 3.0-6.0 (SEBALD, 1956). BOGNER (1968) found that growth of most forest grasses and herbs, including three of the species in this study, was pH related but higher when nitrogen was supplied mainly as

TABLE V. — *Stepwise multiple regression analysis (F-test >4, n=17−20) with concentrations of leaf elements as dependent variables and soil pH, base saturation, organic matter and clay content as independent variables. For leaf-Ca, Mg, Na, K, Mn and Zn the corresponding soil element was included as an independent variable. Only the first entered variable is noted with the sign of the correlation, other variables with* (○).

	Leaf concen-tration	pH	Base satu-ration	Orga-nic matter	Clay	Other	R^2	
							1st	Total
Mercurialis perennis	Ca				○	+Ca	89	92
	Mn		−			Mn	74	92
	Mg	○				Mg	49	61
	Al	−					44	44
	Sr	+					44	44
	P			−			39	39
	K				+		25	25
	Zn				+		22	22
Galium odoratum	Sr	+			○		62	78
	Mn	−				Mn	61	70
	Mg		−			Mg	40	66
	S				−		45	45
	Na				−		40	40
	N						37	37
	K	+					23	23
	B			+			21	21
	Zn					+Znsat	21	21
Stellaria nemorum	Mn		−				69	69
	Ca		+			Ca	22	47
	N			+			45	45
	S			+			39	39
	K	+					38	38
	Na					+Na	29	29
Maianthemum bifolium	Mn		−			Mn	33	72
	Mg			+			53	53
	Na			−		Na	36	51
	Ca				+		41	41

nitrate. This probably means that in natural and quite acidic conditions, species do not reach their maximum potential growth. In this study, the cover of *M. perennis* and *G. odoratum* increased with pH. *S. nemorum* had a maximum cover at intermediate and *M. bifolium* at lower pH values. The height and number of shoots showed the same relationships as cover.

As shown in an earlier study (FALKENGREN-GRERUP, 1989 *c*), a high organic matter content of the soil seems to be negative for many forest herbs, independent of soil acidity. The growth of *M. bifolium* was, however, positively related to organic matter content for most parameters, including flowering. *M. perennis*, on the other hand, even though growing on less organic soils, seemed to react negatively with both a lower flowering frequency and a smaller number of shoots produced by a rhizome. Other soil properties of importance were exchangeable amounts of K to *S. nemorum*, Na to *G. odoratum* and clay content to *M. perennis*.

TABLE VI. — *Stepwise multiple regression analysis (F-test>4, n$=17$-20) with biometric measurements as dependent variables and all measured soil properties and leaf concentrations of nutrients as independent variables. The first entered variable is noted with the sign of the correlation, other variables with* (○). Significant (F>4.0) *multiple correlation coefficients are shown for the first variable and for all variables entered.*

	SOIL							LEAF						R^2	
	Organic matter content	Clay	Na	K	Ca	Zn	Other	Sr	Mg	Na	Mn	N	Other	1st	Total
Mercurialis perennis															
No. of shoots m^{-2}		○						○		–			K	51	90
Shoot height		○									–		S	45	79
No. of shoots rhizome^{-1}	–													25	25
No. of leaves								+						39	39
Flowering	–													32	32
Small plot cover	○	○						○		–				50	86
Shoot × height		+						○		○			A l	35	88
Galium odoratum															
No. of shoots m^{-2}			+											63	63
Shoot height	○	+							○					49	82
No. of shoots rhizome^{-1}													+P	49	49
No. of leaves														ns	ns
Flowering					+									27	27
Small plot cover			+									○		56	67
Shoot × height			+											75	75
Stellaria nemorum															
No. of shoots m^{-2}					○							–		26	45
Shoot height							+Mg, Mn							65	76
No. of shoots rhizome^{-1}				○		+					○			38	76
No. of leaves														ns	ns
Flowering				+										25	25
Small plot cover									–				S, B	57	84
Shoot × height				+					○					50	68
Maianthemum bifolium															
No. of shoots m^{-2}	+												Fe	70	82
Shoot height											–			20	20
No. of shoots rhizome^{-1}					○	○	+pH							26	55
No. of leaves	+													20	20
Flowering	+													35	35
Small plot cover	+												Fe	70	82
Shoot × height	+												Fe	75	84

Flowering frequency was related to soil variables for all four species, but the multiple correlation coefficients were relatively low. Other factors are probably more important for flowering. Cover of many deciduous forest species decreases with increased canopy cover (TYLER, 1989) and flowering is probably even more sensitive to reduced light. Other studies show that flowering of *O. acetosella* was higher at 27% of full daylight than at 6% (PACKHAM, 1978) and that the flowering of *M. perennis* also was retarded at lower light irradiance (MURKERJI, 1936).

The importance of the structural and chemical properties of the soil has been described in this study. The variation in growth and flowering follows a specific pattern in a pH-gradient, that also encompasses the structural changes into mor soils. The study gave fundamental information on the species properties and a basis for future detailed studies.

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